NeoBiota 73: 57–85 (2022)
doi: 10.3897/neobiota.73.80343
https://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Early-phase colonisation by introduced sculptured resin bee (Hymenoptera, Megachilidae, *Megachile sculpturalis*) revealed by local floral resource variability

Jovana Bila Dubaić[1], Milan Plećaš[1], Jovana Raičević[1], Julia Lanner[2], Aleksandar Ćetković[1]

1 *Faculty of Biology, University of Belgrade, Studentski trg 16, 11000 Belgrade, Serbia* **2** *University of Natural Resources and Life Sciences, Vienna; Department of Integrative Biology and Biodiversity Research; Institute of Integrative Nature Conservation Research, Gregor Mendel Str. 33, A-1180 Vienna, Austria*

Corresponding author: Jovana Bila Dubaić (jovanabila@bio.bg.ac.rs)

Academic editor: Sven Bacher | Received 21 January 2022 | Accepted 12 April 2022 | Published 11 May 2022

Citation: Bila Dubaić J, Plećaš M, Raičević J, Lanner J, Ćetković A (2022) Early-phase colonisation by introduced sculptured resin bee (Hymenoptera, Megachilidae, *Megachile sculpturalis*) revealed by local floral resource variability. NeoBiota 73: 57–85. https://doi.org/10.3897/neobiota.73.80343

Abstract

There is a growing interest to document and better understand patterns and processes involved in non-native bee introductions and subsequent colonisation of new areas worldwide. We studied the spread of the East Asian bee *Megachile sculpturalis* in Serbia and south-eastern Europe; the bee was earlier established in the USA (since 1994) and western Europe (since 2008). Its establishment in Serbia remained dubious throughout most of 2017–2019, following its first detection. We hereby report on its establishment and spreading, which were corroborated in 2019 under specific circumstances. Owing to an exceptionally poor blooming of *Styphnolobium japonicum* in 2019, we recorded a high activity density of *M. sculpturalis* concentrated on a scarce key food resource. We present a novel quantitative approach for an improved early detection of *M. sculpturalis*, based on the interplay between the bee local occurrence pattern and dynamics of key food-plant(s) availability. This approach seems particularly effective during the early-phase colonisation, at initially low population density of introduced bees. We address the importance of integration of the genuine plant usage patterns with context-specific bee assessment options in establishing effective monitoring. The improved understanding of *M. sculpturalis* local dynamics triggered the questions about possible origin(s) and modes of its dispersal east of the Alps. To explore the possible scenarios of *M. sculpturalis* introduction(s), we extended the study to a wider spatio-temporal context – the region of SE Europe (2015–2019). The two complementary study approaches (at local and regional scale) provided more comprehensive evidence of bee dispersal history and the detection patterns in varied recording

Copyright *Jovana Bila Dubaić et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

contexts. Based on this two-scale approach, we suggest that a diffusive mode of *M. sculpturalis* introduction into Serbia now seems to be a more plausible scenario (than a long-distance jump). We argue that the integration of outcomes from the contrasting approaches (a systematic surveillance, based on plant resources and a broad-scale opportunistic recording) could be of great methodological relevance for the development of future monitoring protocols.

Keywords

colonisation scenarios, invasive pollinators, monitoring, non-native bees, Serbia, south-eastern Europe, *Styphnolobium japonicum*

Introduction

Amongst the continually growing number of introduced species being discovered around the world (Seebens et al. 2017; Pyšek et al. 2020), bees as a group (Hymenoptera, Apoidea, Anthophila) may count as moderately large. There are about 80 species worldwide found outside their native ranges (Russo 2016), representing a small share of an estimated total of more than 20,000 extant bee species (Michener 2007; Ascher and Pickering 2020). The majority of non-native bees (around 73%) were established following accidental introductions, with a remarkable number of those that are cavity-nesters, principally in various types of wooden material or hollow plant stems (Russo 2016; Poulsen and Rasmussen 2020). Most of the introductions happened in North America (around 69%), while Europe could be currently regarded as a comparatively "coldspot" of alien bee species richness. Of only three fully-confirmed non-native bee species in Europe, two are still known from quite restricted areas: *Megachile disjunctiformis* Cockerell, 1911, in central Italy (only Bologna) and *Xylocopa pubescens* Spinola, 1838, in southern Greece and southern Spain (Rasmont et al. 2017; Bortolotti et al. 2018). So far, *Megachile sculpturalis* Smith, 1853 is the only alien bee widely established and continuously spreading across Europe.

A growing number and geographical extent of alien bee introductions worldwide raise concerns regarding their potential to cause negative environmental impacts. Documented or predicted impacts include: decline of native bee populations through competition (for floral or nesting resources) or pathogen and parasite transmission, degradation of native flower-pollinator networks, reduced pollination of native and crop plants, facilitation of alien weeds and invasive plants (Goulson 2003; Russo 2016; Morales et al. 2017; Vanbergen et al. 2018; Aizen et al. 2020). So far, detrimental effects caused by alien bees were clearly established in a relatively few cases – principally by representatives of social bees: *Apis mellifera* L. and *Bombus* spp. (Russo 2016; Morales et al. 2017). Much less common are studies that quantitatively document possible negative impact of solitary alien bees (MacIvor and Packer 2015; Fitch et al. 2019; LeCroy et al. 2020), including the recent survey on *M. sculpturalis* (Geslin et al. 2020). Although these results were mostly based on correlational evidence, the lack of indisputable interaction amongst native and non-native bees should not be interpreted

as the lack of impact (Stout and Morales 2009). In the case of *M. sculpturalis*, its most worrying feature is an unusually aggressive and/or destructive behaviour exerted while competing with native solitary bees for nesting cavities (summarised in: Le Féon et al. 2018; Lanner et al. 2020a, 2020b; Straffon-Díaz et al. 2021). This competition may be both direct (aggressive repelling or even destruction of brood of other bees in already closed nests) or indirect (exploitative competition for nesting cavities), including the elements of amensalism (e.g. killing of co-occurring species that are using the cavities of different size-classes, i.e. not being in competition). However, there are still no exact and straightforward estimates of its extended impact on affected taxa, i.e. the conclusive evidence of causative effects on population trends. Following the environmentalist's precautionary principle, it may be best considered as a potentially invasive alien species (Bila Dubaić et al. 2021), pending further studies. In this context, we use the term "invasive" in its restricted conservationist sense, i.e. to denote a subset of all established alien species that cause substantial negative impact on native biota and/or ecosystems (e.g. Russo 2016; Vanbergen et al. 2018; IUCN 2020). In some other studies on this bee, the term was used somewhat more loosely or in a wider sense – according to the approach to include all alien species that are rapidly/extensively expanding in the non-native range, regardless of impacts (cf. Blackburn et al. 2011; Hui and Richardson 2017; for conceptual and terminological controversies in invasion biology, see also: Hoffmann and Courchamp 2016; Courchamp et al. 2017).

Megachile sculpturalis belongs to the subgenus *Callomegachile* Michener, which is distributed principally in the Old-World tropics (Michener 2007; Ascher and Pickering 2021). As a rare extratropical member, *M. sculpturalis* range stretches across eastern Asia: from Taiwan and eastern mainland China, through Korean Peninsula to Japan (Batra 1998; Wu 2006; Ascher and Pickering 2021). It is a bee of a distinctive appearance – quite large, parallel-sided black body, 21–27 mm long in females and 12–22 mm in males (Hinojosa-Diaz et al. 2005; Aguado et al. 2018), wings transparent with dark tips (a comprehensive description is available in Sheffield et al. 2011). Females make nests in existing cavities in dead wood or hollow plant stems and seal them with resin-like material (Hinojosa-Diaz et al. 2005; Maeta et al. 2008; Quaranta et al. 2014; Westrich et al. 2015), hence the colloquial name initially coined for this bee in North America: "giant resin bee"; here, we adopted a more appropriate alternative name: "sculptured resin bee" (from: iNaturalist.org). It is assumed that long-distance overseas introductions of this cavity nester have happened via inadvertent importation of timber goods or other suitable nesting materials (Mangum and Brooks 1997; Quaranta et al. 2014; Russo 2016; Le Féon et al. 2018). A similar mechanism (passive, human-assisted transportation) is expected to contribute to secondary introductions within colonised continents, as long- or short-distance jumps (Westrich et al. 2015; Lanner et al. 2020a). Due to a large size, contrasting dark and bright colour-pattern, vivid nesting activity and frequent visitation of some commonly-available ornamental plants, this bee is readily spotted and recognised and, hence, expectedly easy to be detected as soon as it appears in new areas (Quaranta et al. 2014; Lanner et al. 2020a).

The first confirmed establishment outside of *M. sculpturalis* native range was in 1994 in North Carolina, USA (Mangum and Brooks 1997), followed by a rapid expansion across the eastern half of North America (Mangum and Sumner 2003; Hinojosa-Diaz et al. 2005; Parys et al. 2015). In Europe, it was first detected in 2008, in south-eastern France (Vereecken and Barbier 2009); this was soon followed by records from north-western Italy in 2009 and south-eastern Switzerland in 2010 (Amiet 2012; Quaranta et al. 2014). Documented spreading in the period 2011–2014 was mostly confined to these areas (Westrich et al. 2015; Le Féon et al. 2018; Ruzzier et al. 2020). Since 2015, a more dynamic range extension took place: around the Alps in Switzerland, southern Germany, Slovenia, Austria and Liechtenstein (Westrich et al. 2015; Dillier 2016; Gogala and Zadravec 2018; Lanner et al. 2020a; Westrich 2020), much more widely in France and Italy (Le Féon and Geslin 2018; Le Féon et al. 2018; Poggi et al. 2020; Ruzzier et al. 2020), south-westwards into NE Spain (Aguado et al. 2018; Ortiz-Sánchez et al. 2018) and, most recently, across the Mediterranean Sea, reaching the Island of Mallorca as the southernmost point in Europe so far (Ribas Marquès and Díaz Calafat 2021). In contrast with this largely continuous spreading (comprising also few smaller jumps), the range establishment east of the Alps (2015–2019) represents more remote, arguably long-distance dispersal events of yet unclear origin and mechanisms: into north-eastern Hungary (Kovács 2015), north-eastern Austria (Westrich 2017), northern Serbia (Ćetković and Plećaš 2017), southern Croatia (Resl 2018; "pitrusque" 2019), Crimea (Ivanov and Fateryga 2019), southern Romania (Hymenopterists Forum 2019) and northern Bosnia & Herzegovina in 2020 (Nikolić 2020). The range expansion within Europe for the reference period (2008–2019) is presented schematically with a series of phase-maps and a summarising review of its dynamic distribution (Ćetković et al. 2020; Suppl. material 1).

Following its remarkable non-native spreading, evidence was accumulated about sculptured resin bee interactions with numerous plant genera and families (Quaranta et al. 2014; Parys et al. 2015; Le Féon et al. 2018; Ruzzier et al. 2020), showing a more diverse spectrum than currently available for its native area. Accordingly, *M. sculpturalis* is often referred to, or assumed to be polylectic (Mangum and Brooks 1997; Maeta et al. 2008; Quaranta et al. 2014; Parys et al. 2015; Westrich et al. 2015; IUCN 2020; Ribas Marquès and Díaz Calafat 2021), but without clear evaluation of the documented visitation pattern, for example, the share of pollen vs. only nectar foraging. Based on numerous sources (cf. Ćetković et al. 2020; an ongoing analysis), *M. sculpturalis* shows a particularly strong preference for the pollen of Fabaceae (Batra 1998; Mangum and Sumner 2003; Maeta et al. 2008; Westrich et al. 2015; Campbell et al. 2016; Dillier 2016; Hall and Avila 2016; Aguado et al. 2018; Andrieu-Ponel et al. 2018; Le Féon and Geslin 2018; Le Féon et al. 2018; Guariento et al. 2019; Ruzzier et al. 2020; Westrich 2020; Ribas Marquès and Díaz Calafat 2021), principally of large-flowered members of the subfamily Faboideae. Within the European range, the most frequently documented pollen-source is the ornamental Japanese pagoda tree, *Styphnolobium japonicum* (L.) Schott. In contrast with this growing evidence, the loosely repeated "wide polylecty" might represent a biased or uncritical perception, which ignores often remarkably narrow effective

dietary preferences of *M. sculpturalis*. The patterns of genuine plant usage of this bee are yet to be thoroughly evaluated, taking into account the floral resource availability, the variability of plant phenology, as well as the suitability of different habitat types across the colonised areas. Undoubtedly, *M. sculpturalis* is quite opportunistic in its foraging for nectar sources, but much more selective when provisioning the pollen for its brood.

Despite a growing number of studies, a specified approach is still missing to quantify the sculptured resin bee distribution dynamics and population trends, its interactions with key plants and native bees and, hence, ultimately, to assess its invasive potential. As a first step, we need an effective approach for early detection and extended surveillance of its expansion. To address these questions, we explored the spatial relationships between bee activity patterns and local availability of key plant resources. We present the survey of the sculptured resin bee introduction in Serbia as an event-driven case study of an early-phase colonisation. Initially, the accidental encounter of a single specimen early in 2017 was interpreted as a likely long-distance chance dispersal of uncertain success (Ćetković and Plećaš 2017). After an extended lack of confirmation throughout the seasons of 2017–2018, the current study was initiated with the second find in the same area (the city of Belgrade), attained late in 2019 under specific circumstances: owing to an extremely reduced blooming of its preferred host plant (*S. japonicum*) in that year, we managed to detect a vivid activity of still locally-rare sculptured resin bees, temporarily concentrated on a scarce food source. We evaluated the effects of variable floral resources on the sculptured resin bee detectability and developed a quantitative approach for an integrated assessment of the plant availability and bee local density, as a step towards a more comprehensive monitoring. The improved understanding of *M. sculpturalis* local dynamics further triggered the questions about the origin(s) and modes of its dispersal east of the Alps (since 2015; cf. above), which were not appropriately addressed elsewhere. Therefore, we extended the study to a wider, regional-scale context, to consider possible scenarios of *M. sculpturalis* introduction(s) and to reveal its early colonisation dynamics within the SE Europe region. The two-scale study (local and regional) should provide a much wider complementary evidence from the methodologically different approaches across the spatio-temporal scales, aiming to relate the bee dispersal history to the detection patterns on a more comprehensive basis. Therefore, we expect that outcomes would be highly relevant for the development of standardised monitoring protocols.

Material and methods

The study of *M. sculpturalis* arrival and establishment in Serbia was mostly based on extensive fieldwork within the city of Belgrade, during the period of 2017–2019. The wider geographical and temporal context of this survey included principally the eastern Pannonian Plain, but we also considered the nearest known occurrences towards the west and east of this area (from Austria and Slovenia through the Crimean Peninsula), for the period of 2015–2019.

Local scale: Belgrade as the study area

Belgrade is one of the largest cities in south-eastern Europe (Belgrade "proper" administrative-urbanistic core area is nearly 776 km^2, population > 1.5 million), situated at the border between the two quite different geographical units: the predominantly hilly to mountainous Balkan Peninsula to the south and the vast lowlands of the Pannonian Plain to the north. It is positioned in a climatically transitional zone between the temperate-continental and the more steppic regime, with a relief spanning the altitude range of 65–506 m. The Belgrade area encompasses more than 50% of varied agricultural habitats as a matrix, with embedded mosaics of urban and rural habitats; two principal sections of Belgrade (the Balkan and the Pannonian – Fig. 1) are characterised by a distinct spatial arrangement and contrasting types of settlements, agricultural systems and more natural habitats, owing to a largely different physiography and historical development. From the perspective of wild bee studies, various urbanistic areas may be characterised by differing types, extent and relative share of suitable habitats (e.g. from urban green to semi-natural). In order to consider possible coarse-scale effects of variability in key resources and other environmental features across urban gradients of Belgrade, we used a framework of wider "urbanistic zones" (Fig. 1). They are based on landscape scale characterisation of available elements of physiography, land-cover, gradients of urbanisation and management regime features. Some easily-defined coarse-scale differences (e.g.

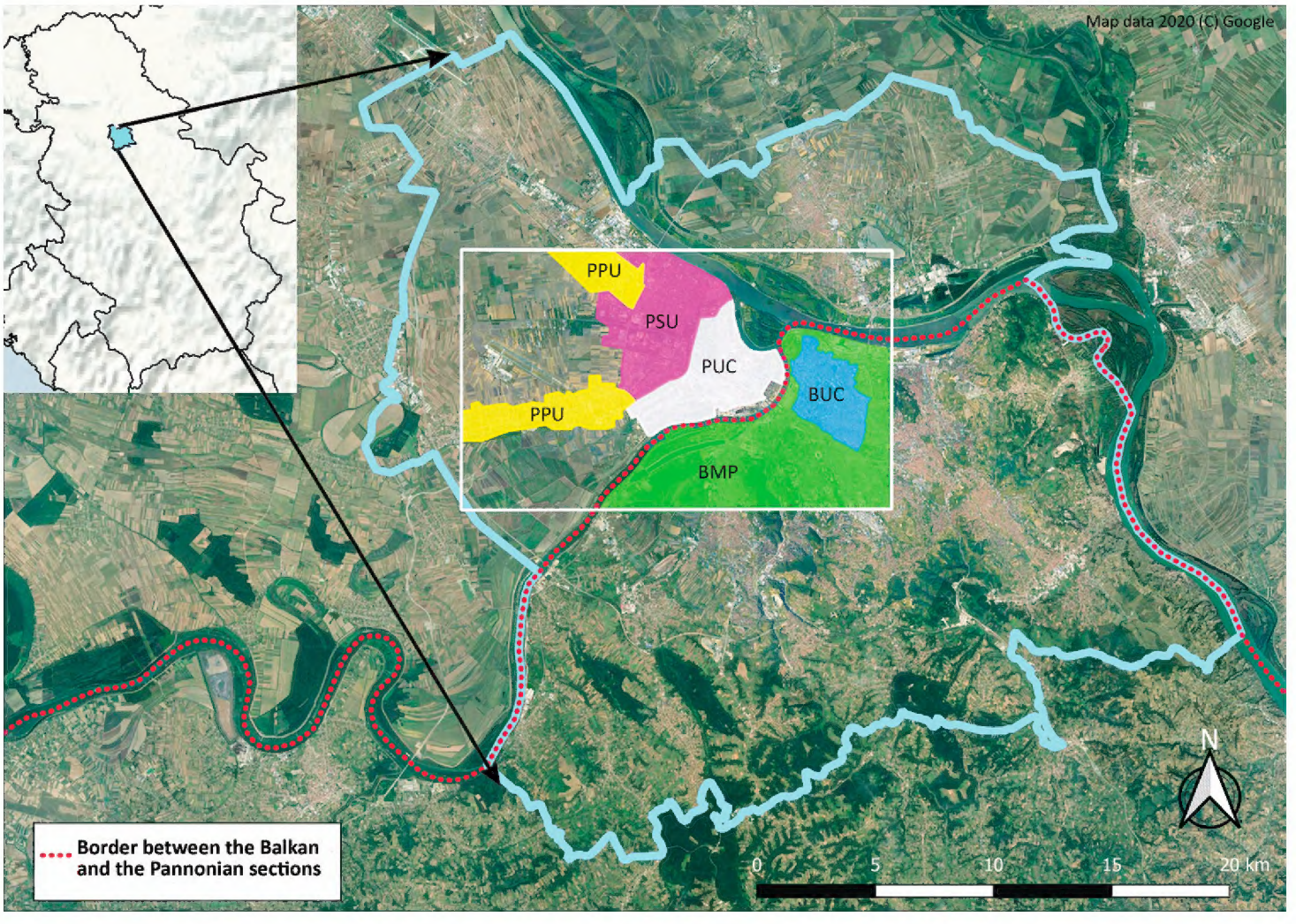

Figure 1. Landscape/urbanistic zonation of the study area in Serbia (18×11 km), within Belgrade proper (light blue outline; sections separated by the red dotted-line): BUC – Balkan Urban Core; BMP – Balkan Mixed Periphery; PUC – Pannonian Urban Core; PSU – Pannonian Semi-Urban; PPU – Pannonian Peri-Urban.

varied urban temperature regimes or dominant management practices) might differently affect activity patterns of plants and bees, potentially leading to dynamic shifts in bee local distribution and resource usage. More details on the wider study area and operative aspects of zonation used in this survey are available in Suppl. material 2: Figs S2.2–S2.23.

Local scale: survey set up and study design

The first record of *M. sculpturalis*, in early July 2017 (a single male), was an unexpected find within a routine monitoring of wild bee communities of selected urban habitats in the Belgrade area (Ćetković and Plećaš 2017; Fig. 2A). However, its establishment in Serbia remained unconfirmed during the first two seasons. We extended efforts to explore the state of its presence, focusing on locations with the Japanese pagoda tree (*Styphnolobium japonicum*), which is the most favourable pollen source for *M. sculpturalis* in Europe. This exotic plant is probably the only species with both an appropriate blooming phenology and a high density throughout the Belgrade area. During the seasons of 2017–2018, our surveys covered 12 locations within 18 days (26 "occasions" = unique date/location combinations), spending about 440 person-minutes (= 7.25 person-hours) in collecting or observing bees on *S. japonicum* throughout the area and covering the *M. sculpturalis* main flight period. At the same time, we continued with variously focused wild bee surveys on other abundant summer-blooming plants across Belgrade. This included an extensive survey on *Lavandula* and *Ballota* (Lamiaceae) and sporadically on *Buddleja* (Scrophulariaceae) – all being listed as attractive food plants for *M. sculpturalis*, at least as nectar sources (Quaranta et al. 2014; Le Féon et al. 2018; only *Ballota* was documented as a pollen source, cf. Ivanov and Fateryga 2019). For observations on *Lavandula* (8 locations within 18 days, 21 unique occasions, totalling nearly 490 person-minutes) and *Ballota* (13 locations within 27 days, 32 unique occasions, totalling > 1,190 person-minutes), we spent about 28 person-hours during the summer seasons of 2017–2019. None of these efforts yielded any additional point-occurrences or recorded interactions of *M. sculpturalis* (for *Buddleja* see Results).

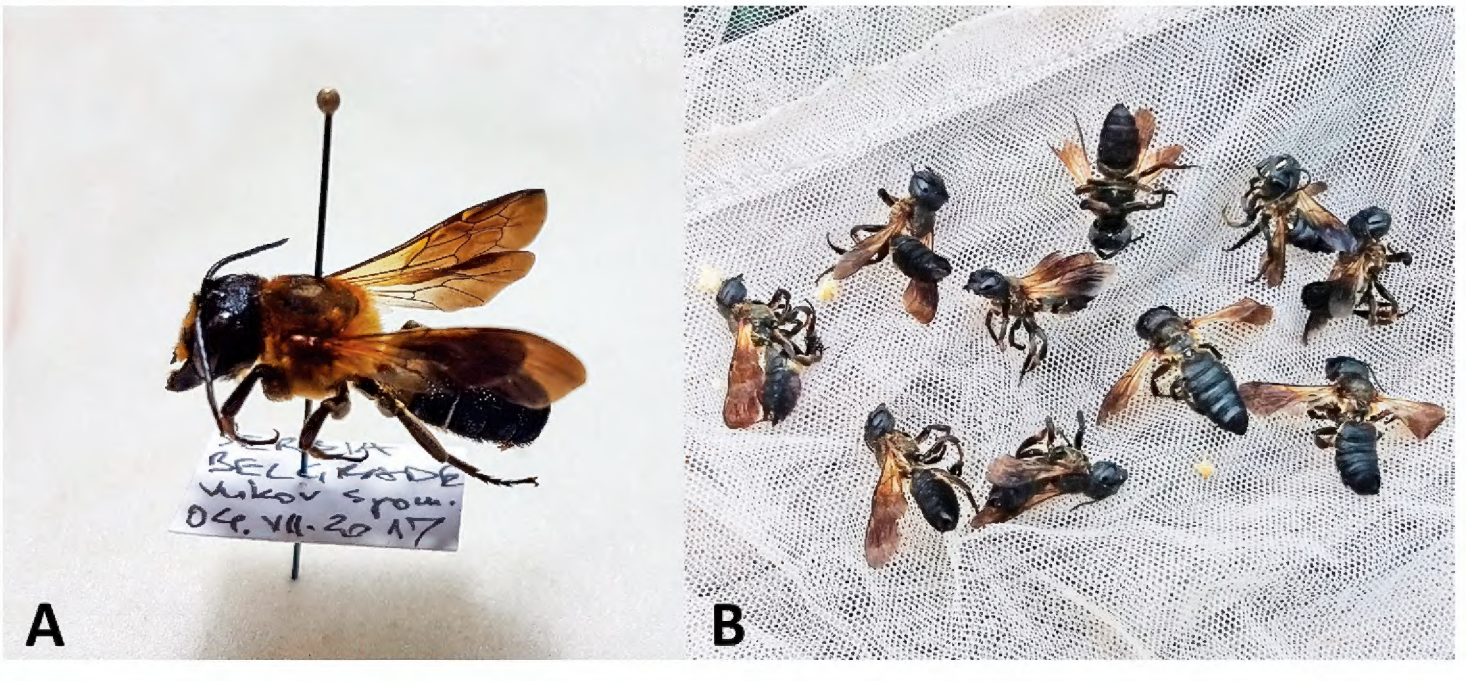

Figure 2. A the first specimen of *Megachile sculpturalis* (male), caught in Serbia in July 2017 **B** mass-foraging females detected in August 2019.

The second record of *M. sculpturalis* was also accidental. The summer of 2019 was characterised by an extreme failure in *S. japonicum* blooming (see details in Results); for this reason, this plant was excluded from our regular monitoring that year. Then, upon an unexpected detection of numerous sculptured resin bees on 2 August 2019, on a single *S. japonicum* tree (Fig. 2B; Suppl. material 3: Table S3.2), we undertook an immediate survey across Belgrade to document and quantify its confirmed presence. We searched for and checked as many locations with *S. japonicum* as possible, across all urbanistic zones (Fig. 1; see also: Suppl. material 2: Fig. S2.3). However, the next 7-day period (3–9 August) represented the very end of the *S. japonicum* blooming season in 2019, when many trees had already ceased blooming.

On all locations with still-blooming trees, we conducted estimation of bees foraging on flowers, using binoculars where needed (for high crowns). Due to different situations amongst the sites as well as logistic constraints, the duration of work at each location varied from 1–50 minutes (mostly ranging 10–20, mean ~ 15.3 ± 10.7 SD). The estimation procedure was adjusted to varied levels of activity density: (**a**) at sites with lower activity (≤ 5 observable individuals), bees were usually not present continuously during the observation; here, we used timed counts to quantify the presence of foraging bees on a tree and, if the number of individuals was changing over the period of observation, we split the total time into intervals characterised by each recorded value (0–5); (**b**) when continuous and more vivid activity was observed (> 5 bees visible at any moment), 3–4 snapshot counts were made over the time spent on site, using two abundance classes: moderate (6–10) or high (11–20). We adapted the snapshot technique used in ornithology (Gaston et al. 1987; Greene and Efford 2012; Barraclough 2020), which proved suitable for situations when numerous individuals are flying within the field of view, without the possibility to count them accurately. At a few sites with variable bee activity on different trees, the combination of both techniques was employed. To enable standardised comparisons, we scaled all recorded values to one minute of continual bee activity on a defined unit of floral resource within a landscape sector (as elaborated further on), by averaging all counts against the recorded time (hereafter Bees per Minute = BpM). Details of recording and calculation procedures are available in Suppl. material 3 (explanation of metrics in Table S3.1; sampling duration and BpM estimates per sectors in Table S3.2). In total, we spent about 300 person-minutes (5 person-hours) working on 16 sites with at least some blooming trees (out of 40 surveyed sites), mostly observing and counting (> 260 minutes). At some sites, we also collected bee specimens by hand-net, as vouchers and for future genetic studies.

Simultaneously, we estimated the key floral resource to assess if its quantity, distribution and phenology affect the local differences in activity density and distribution of the bee population. We recorded the number of *S. japonicum* trees (hereafter NoT) and visually assessed their actual blooming status at each visited location: the number of trees that entered blooming in 2019 (hereafter NoT_iB), the share of inflorescences developed on each crown in bloom during 2019 (as a fraction of the fully-blooming crown; summed value interpreted as Total Floral Resource, hereafter TFR) and, finally, the actual share of flowers still in bloom on each crown at the moment when we made the observation

(summed to Current Floral Resource, hereafter CFR). We continued to survey *S. japonicum* until early September, regardless of the ceased blooming (and no bee activity), to provide the spatial coverage of resource availability across the study area. For extended explanations and visual examples of these parameters, see in Suppl. material 3: Table S3.1.

All surveyed locations were primarily georeferenced in Google Earth Pro ver. 7.3.3.7786 (Google Inc. 2020) and further prepared as distribution maps in QGIS ver. 3.4 (QGIS Development Team 2018). To deal with the uneven and patchy distribution of surveyed *S. japonicum* trees and the logistic limitations of the sampling approach, we grouped the point-sampled quantitative data following the rationale similar to landscape ecology studies on wild bees (e.g. Steffan-Dewenter et al. 2002; Steckel et al. 2014; Cohen et al. 2020). We defined a primary framework of circular sectors with 250 m radius (hereafter: S250; Suppl. material 2: Fig. S2.3A), manually fitted to include all surveyed point-locations without overlapping. Various bees perceive the landscape composition and configuration (particularly distribution of resources and other habitat features) at different spatial scales, since their foraging ranges depend principally on size; the radius of 250 m is commonly used to define the smallest meaningful study scale (Steffan-Dewenter et al. 2002), while larger-bodied bees may forage at much larger distances (Gathmann and Tscharntke 2002; Greenleaf et al. 2007). Due to spatial limitations of the sampled area, we added only one coarser scale (sectors of 500 m radius, hereafter S500; Suppl. material 2: Fig. S2.3B) to test for different scale effects. As a result, all recording sites were arranged into two series of standardised circular sectors: 40 locations S250 (ca. 0.2 km^2) and 23 locations S500 (ca. 0.8 km^2); all parameters were calculated per those spatial units (see more details about the procedure in: Suppl. material 2: Fig. S2.3). Therefore, we used some technical concepts and experiences from landscape ecology studies as a suitable practical approach (and a prospective "working framework") to quantify and analyse relationships between bee distribution patterns and resource availability.

All values from field assessments were summed per defined sector. To calculate TFR, we summed individual values from each *S. japonicum* tree in bloom, expressed as a fraction of the whole crown, based on the estimated maximal extent of blooming attained during the summer of 2019. Similarly, we calculated CFR as a sum of estimated blooming fractions at the moment of assessment; this represents the actual extent of blooming of each crown within the sector. We recorded blooming fractions as percentage of the whole crown for each assessed tree and then summed the values in decimal form (e.g. blooming of 10% of one crown, 25% of another and 80% of a third gives the value of 1.15 "unit crowns" per sector; more details and visual examples for the calculation available in Suppl. material 3: Table S3.1, summed results in Table S3.2).

Local scale: statistical analyses

We tested if various aspects of floral resource distribution and seasonal dynamics (i.e. change from TFR to CFR level of blooming) had a measurable effect on local differences in bee activity. We analysed the relationship between the bee activity den-

sity (BpM) and all measured parameters of the key floral resource (NoT, NoT_iB, TFR and CFR), calculated in S250 and S500 frameworks, with the Generalised Least Square (GLS) linear regression, to account for heteroscedasticity of errors. Additionally, we used GLS linear regression to analyse the relationship between BpM and TFR, CFR, percentage of TFR (TFR/NoT) and percentage of CFR (CFR/NoT), all averaged for each urbanistic zone. Analyses assumptions were tested by examination of residuals. Furthermore, we tried to establish if there were any local patterns in reduction of *S. japonicum* blooming (i.e. any possible differences caused by environmental effects that specifically vary with urbanistic gradients, using urbanistic zones as tentative proxies) and, if so, are the bees responding to these differences. Differences in NoT, NoT_iB, TFR, CFR and BpM between urbanistic zones were analysed by the Kruskal-Wallis test. All analyses were performed in R v.3.6.3 (R Core Team 2020) and the R-package nlme v.3.1-144 (Pinheiro et al. 2020).

Regional context: introduction and expansion within SE Europe

We compiled, from all available sources (Suppl. material 4: Table S4.2), a total of 14 occurrences of *M. sculpturalis* from the region most adjacent to the focal study area (Belgrade) – N Serbia and E Hungary (i.e. the eastern Pannonian Region), spanning the period of 2015–2019. Furthermore, we aimed to consider the spatio-temporal correspondence of eastern Pannonian records with the nearest records towards the west (i.e. towards the introduction core of Europe): we included 11 most adjacent records that are very broadly marginal to the wider Pannonian periphery: from E Austria, Slovenia and SW Croatia (2016–2019). Additionally, we considered the rare documented occurrences east of Serbia: one record from Romania (2019) and two records from the Crimean Peninsula (2018–2019). Therefore, we have covered, in a very broad sense, the area of SE Europe, wherein the colonisation by this species was documented only since 2015. Noteworthy, most records from Hungary after 2015 were discovered through a tailored web data extraction within the nationally based internet sources (previously being poorly accessible due to a language barrier). Findings from Serbia also became available with a delay; in the case of the record from Palić of 2018 (northernmost Serbia), it was due to a misidentification (at: Insekti Srbije 2018; corrected in 2020 by JBD).

The compilation and mapping of records were conducted within a more extensive Europe-wide survey of *M. sculpturalis* distribution and expansion; preliminary results for the period of 2008–2019 were presented as series of summary phase-maps in Ćetković et al. (2020) (available at: https://srbee.bio.bg.ac.rs/english). We herewith include a somewhat modified version of the summary map for 2019 (Suppl. material 1), with the regional records clearly delimited within the European distribution. All relevant details – data and metadata (coordinates, dates, bionomics, sources) used for this regional mini-survey are available in Suppl. material 4: Table S4.1. Records were georeferenced using the combination of Google Earth Pro ver. 7.3.3.7786 (Google Inc. 2020) and QGIS ver. 3.4 (QGIS Development Team 2018). Maps were made primarily with QGIS and the output images were further processed with various picture-editing software. We used the "Ruler" tool in Google Earth Pro to measure the linear

distances between various adjacent occurrences (within and between the years in relation to the sequence of their detections), in order to quantify the basic spatial elements of apparent dispersal outcomes.

Results

Local scale: the Belgrade survey

Following the first detection of *M. sculpturalis* in Belgrade (and Serbia), in July 2017, we confirmed the establishment of this species only in August 2019. Our recording was almost exclusively based on bees foraging on *S. japonicum* trees. The exceptions were the first detected specimen – a male collected on *Trifolium repens* and a single female observed around a *Buddleja* bush; both cases occurred in downtown parks with nearby present *S. japonicum* trees. We did not detect *M. sculpturalis* neither on *Lavandula* nor on *Ballota* during the 2017–2019 period, despite notable efforts.

Most of the metrics calculated within the S500 framework had non-significant values (see in Suppl. material 5); therefore, we herewith present only the results from the S250 framework. Throughout the Belgrade area, we recorded *M. sculpturalis* at most locations where the current floral resource (CFR) of *S. japonicum* was sufficient to attract foraging bees at the moment of survey (Fig. 3A, B). The minimal sufficient value was CFR ≥ 0.1, found in 16 of 40 sectors (40%). Bees were recorded in 14 of 16 suitable sectors (88%); within five locations, we also collected specimens (22 females, 3 males). The estimated activity density of bees per sector ranged from 0 to 15.5 BpM (mean 4.66 ± 5.35 SD). The remaining sectors were recorded as without any blooming in 2019 or with blooming being already finished before our survey; hence, without possibility to detect bees (sectors with values for NoT_iB, TFR or CFR less than 0.05; see in Suppl. material 3). Of all tested metrics, only CFR had a significant effect on BpM (Table 1, Fig. 4A); when the values were averaged for each urbanistic zone, only CFR and %CFR had a significant effect on BpM (Table 2, Fig. 4B). We did not find significant differences in bee activity density amongst different urbanistic zones of Belgrade (H(4) = 4.521, p-value = 0.341).

Table 1. Results of the GLS linear regression models of the relationship of bee activity density (BpM) and variables NoT, NoT_iB, TFR and CFR (N = 16).

Model		Estimate	SE	t-value	p-value
NoT	Intercept	6.368	1.638	3.887	**0.002***
	Variable	-0.144	0.854	-1.644	0.122
NoT_iB	Intercept	6.092	2.001	3.045	**0.008***
	Variable	-0.557	0.579	-0.962	0.352
TFR	Intercept	3.459	2.689	1.286	0.219
	Variable	0.951	1.824	0.521	0.611
CFR	Intercept	-0.154	1.858	-0.089	0.935
	Variable	12.276	3.891	3.154	**0.007***

Significant p-values in bold (* p ≤ 0.01). NoT– number of trees; NoT_iB – number of trees in bloom; TFR – total floral resource; CFR – current floral resource.

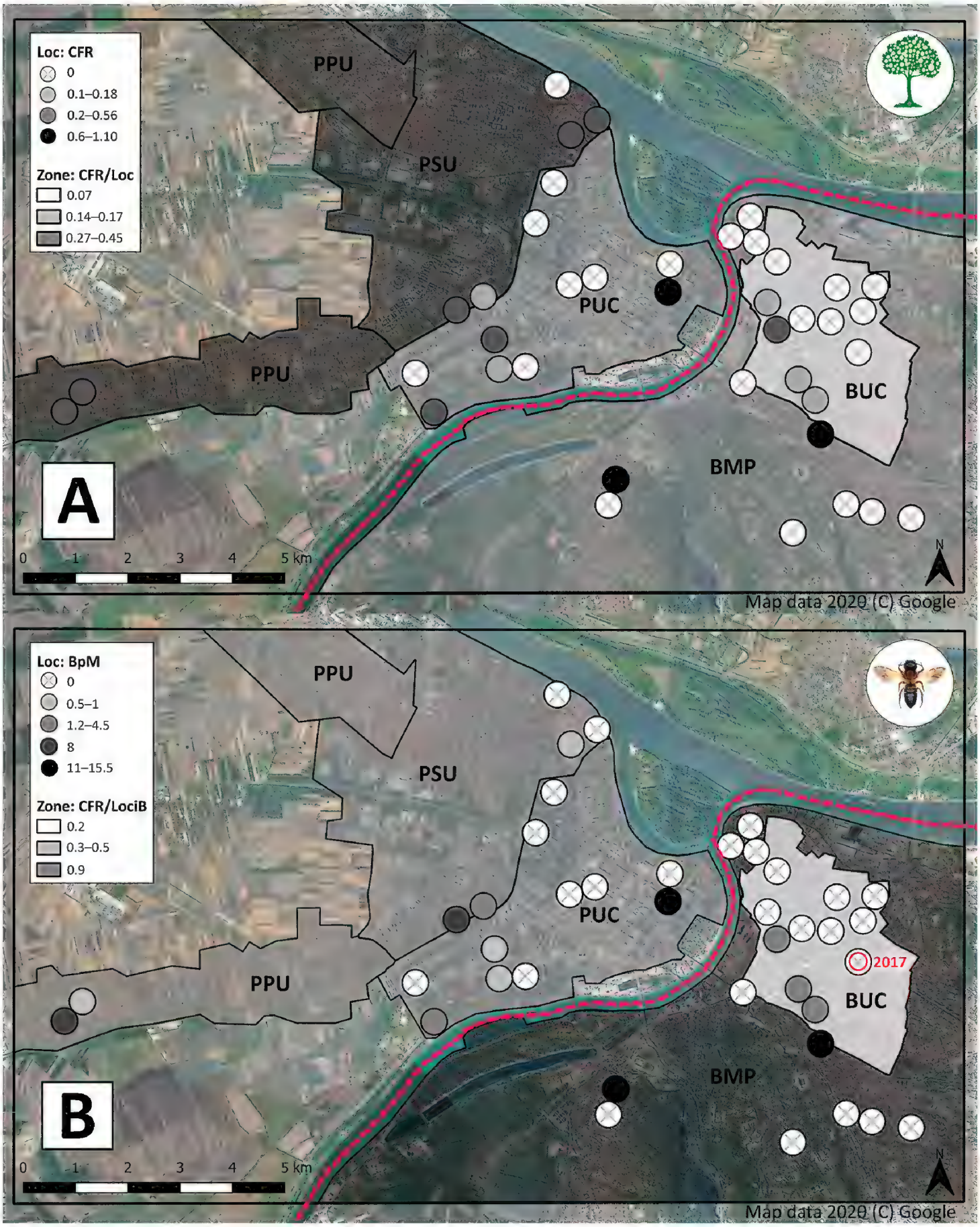

Figure 3. Distribution of **A** effective floral resources of *S. japonicum*, as surveyed in August 2019 (Current Floral Resource – CFR) and **B** respective metrics of *M. sculpturalis* activity density (Bees per Minute – BpM), both presented within the S250 framework (circular sectors – "landscapes" of r = 250 m; values shown in classes). Urbanistic zones (acronyms as in Fig. 1) are shown as background shades of grey, representing the averaged value of CFR per zone calculated either for **A** all 40 sectors or **B** only for 16 sectors with CFR ≥ 0.1. The location of the first find is marked with "2017". Numerical data available in Suppl. material 3: Tables S3.2–S3.4; see also maps in Suppl. material 5 for the complete visualisation of floral resource metrics.

Table 2. Results of the GLS linear regression models of the relationship of bee activity density (BpM) and variables TFR, CFR, %TFR and %CFR, all averaged across each urbanistic zone (N = 5).

Model		Estimate	SE	t-value	p-value
TFR	Intercept	1.575	5.663	0.278	0.799
	Variable	3.121	4.184	0.745	0.509
%TFR	Intercept	0.568	2.388	0.238	0.827
	Variable	15.359	6.196	2.479	0.089
CFR	Intercept	-2.492	0.909	-2.741	0.071
	Variable	18.008	1.838	9.798	**0.002***
%CFR	Intercept	1.293	0.756	1.711	0.186
	Variable	30.223	3.981	7.592	**0.005***

Significant p-values in bold (* $p \leq 0.01$). TFR – total floral resource; %TFR – percentage of total floral resource; CFR – current floral resource; %CFR – percentage of current floral resource.

Within the surveyed area (16×9 km was the approximate span of all visited *S. japonicum* locations; Fig. 3A), we covered all urbanistic zones, with a varying number of surveyed locations between the zones (2–11; see also Suppl. material 2: Fig. S2.3). We counted the total of 490 *S. japonicum* trees (NoT), distributed quite unevenly across the study area (1–64 per sector). In 17 sectors (comprising 196 trees), we recorded no sign of blooming during 2019. Within the remaining 23 sectors, only on 51 trees we recorded at least some level of blooming in 2019 (NoT_iB; 12.2% of the total NoT). These blooming trees had a variable share of crowns effectively in bloom (TFR; 48.4% of the total NoT_iB); expressed per sector, TFR values ranged from 0.2 to 3.0 amongst these 23 sectors. As a reference high value, we established that the long-term average intensity of *S. japonicum* blooming in good seasons is at least ≥ 85% of the total crown volume (based on our observations from the seasons of 2017–2018 and 2020, which included about 60 and 550 individual trees, respectively). Accordingly, the sum of detected TFR available to bees during the summer of 2019 represented at most 5.9% of average *S. japonicum* resource availability in good seasons. At the time of our survey (2–9 August, the extent of available resources (CFR) was further reduced: only about 1.5% of the summed crown volume was still in bloom. The effective floral

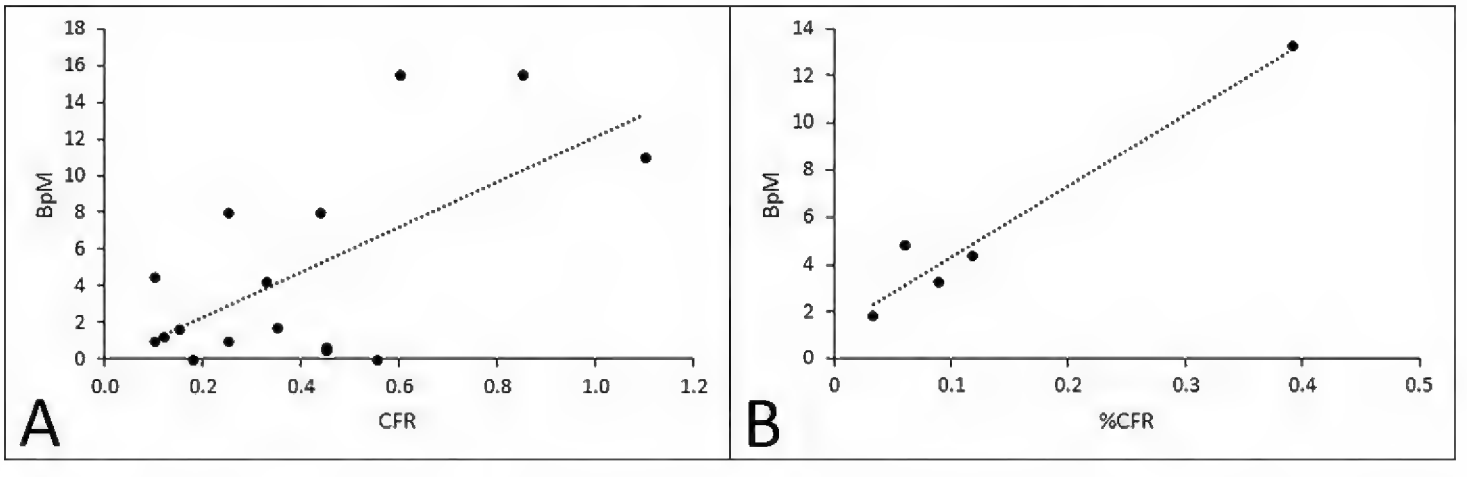

Figure 4. Relationship between **A** BpM and CFR and **B** BpM and %CFR averaged across each urbanistic zone (BpM – Bees Per Minute; CFR – Current Floral Resource; %CFR – percentage of current floral resource).

resources in early August (i.e. values of CFR ≥ 0.1) were recorded in only 16 sectors (totalling about 30% of the respective TFR summed value). Effective CFR values ranged from 0.1 to 1.1 per sector (Fig. 3A). Further details of all metrics are available in Suppl. material 3: Table S3.2, Table S3.3. For the spatial visualisation of established raw patterns, we presented the distribution of all four aspects of resource availability and respective *M. sculpturalis* activity density metrics, in a sequence of maps (Suppl. material 5: Figs S5.1–S5.2). We found no statistically significant differences in any of the floral resource metrics (NoT, NoT_iB, TFR, CFR) between different urbanistic zones (Suppl. material 5: Table S5.1).

Regional context: introduction and expansion within SE Europe

The first record in Serbia (in 2017, in Belgrade) was amongst the earliest known, positioned so remotely to the east from the contemporary colonised areas in western Europe. By that time, the closest previous occurrences were from NE Hungary in 2015 (Kovács 2015; ca. 330 km linear distance to the north) and from NW Slovenia in 2016 (Gogala and Zadravec 2018; ca. 550 km to the west). The closest contemporary occurrence was the first record in NE Austria (Westrich 2017; ca. 490 km northwest of Belgrade). With additional records in 2018, the apparent distribution gap across the eastern Pannonian Plain was reduced to ca. 160 km (from Belgrade northwards to Palić and Szeged). Additional adjacent records to the west (Austria, Slovenia and Croatia) remained at a fairly great distance throughout 2018–2019 (≥ 440 km). Detections further east in Europe (2018–2019) were more distant: ca. 1,000–1,150 km between Crimea (2018) and the closest records in Hungary (2015–2018) or Serbia (2017–2018); ca. 450–530 km between records in Serbia and Romania (2019); ca. 470–510 km between records in Hungary and Romania; ca. 640 km between records in Crimea and Romania. Gaps between the adjacent findings within the E Pannonian Plain were further reduced by the end of the 2019 season (ranging mostly 80–105 km, rarely 115–130 km, but in some areas only ca. 30–40 km), seemingly approaching a near-continuous distribution (cf. summary map in Suppl. material 1; details available in: Suppl. material 4: Table S4.1). Noteworthy, many records from this region were from the nesting situations, while none was from the proven pollen-source plants.

Discussion

We documented and analysed the widespread local occurrence of *M. sculpturalis* within the City of Belgrade, highlighting the early phase of its establishment in Serbia (2017–2019). This initially local case study provided a novel quantitative approach for assessing the bee activity in relation to floral resource availability, contributing to the framework for its early detection. Improved understanding of *M. sculpturalis* dynamic local patterns triggered an extension of the research scope to the wider, regional-scale context of this introduction – the colonisation within the E Pannonian Plain and SE

Europe (2015–2019). The combined outcomes of two complementary approaches, one on local and another on regional scale, provide important elements for future monitoring protocols of this Asian bee.

Local scale: the Belgrade survey

Detection and monitoring of a newly-established species may be challenging before a substantial local population build-up is attained (Hui and Richardson 2017), commonly involving a variously induced time lag after the initial introduction (Crooks 2005). We confirmed the presence of the sculptured resin bee at numerous locations throughout Belgrade in 2019, only two years after its first detection in Serbia. We suggest that such an early and widespread detection was enabled through the effect of "concentration" of bee foraging activities on a limited amount of the preferred floral resource. Namely, the summer of 2019 was characterised by an exceptional reduction of the bee's key food resource (*S. japonicum*): less than 13% of individual trees entered some level of blooming and only about 6% of the potential "blooming volume" was actually in bloom (TFR; as compared with good-blooming years); moreover, the availability of floral resources was further reduced during the short period of our survey (to 1.5%). Therefore, the average bee foraging intensity was concentrated by the factor of nearly 67 (i.e. it was 67 times more likely to observe active bees on inflorescences). Consequently, recording was highly successful: we detected *M. sculpturalis* in 88% of sectors in which the blooming of *S. japonicum* was sufficient to support at least the minimal bee foraging (the threshold value CFR ≥ 0.1 for this study design). The concentration effect may be particularly emphasised when a poor-blooming year follows a good year(s). This is based on a more general mechanism: alternating inter-annual fluctuations of blooming intensity of food plants may promote phase-delayed good or poor reproduction success of affected bee species (Tepedino and Stanton 1981; Crone 2013). Phase-delays produce a mismatch between the actual floral resources and the contemporary bee activity density and, in turn, the alternation of "concentration" and "dilution" effects. Blooming of *S. japonicum* seemingly follows a sort of alternating, but basically more irregular bearing pattern, a phenomenon otherwise well known in numerous tree taxa belonging to widely different plant families (Monselise and Goldschmidt 1982). The good blooming phase of *S. japonicum* in Belgrade during the first two years of *M. sculpturalis* documented presence (2017–2018) was favourable for the establishment and initial population build-up, albeit being slow. However, in the same period, its apparent activity has been diluted over this hyper-abundant and widely available floral resource, making it difficult to detect. We expect that observable activity density of *M. sculpturalis* remains decisively affected by this interplay of concentration and dilution phases, until a substantially abundant local population is attained. The preliminary outcomes from our 2020 survey (reduced recording success in conditions of a good-blooming season) are concordant with this expectation (Bila Dubaić et al. 2021).

Within the sectors with detectable bee activity (CFR ≥ 0.1), we have found that the activity density (BpM) was solely affected and significantly related to the levels

of currently available floral resources (CFR); this was shown at both sector/landscape scale and as averaged values across urbanistic zones defined in this study. We could neither detect any effects of other tested resource parameters (NoT, NoT_iB, TFR) on bee abundance and distribution patterns, nor of other possible environmental features that vary amongst the defined urbanistic zones. Arguably, the lack of significant effects may be, in part, ascribed to a high variability of key floral resources and/or to a small sample size (due to the limited surveying period). However, this may also indicate the ability of *M. sculpturalis* to efficiently trace available key food resources, owing to its size and expectedly strong flight capacity (Quaranta et al. 2014; Westrich et al. 2015). Accordingly, it might be able to quickly optimise its foraging over sizable distances at the local scale, which is of particular importance when resources become critically restricted. Probably for the same reasons, our analysis has shown that a coarser-scale framework (S500) was less meaningful than the finer-scale one (S250), which seems counter-intuitive for such a large bee and, hence, worthy of further testing. Upon *M. sculpturalis* reaching higher, more stable abundances, it will be of interest to examine if other aspects of urban environmental gradients might also affect its local distribution and activity patterns (in addition to the key food availability). Of various features of urban environments, commonly emphasised as affecting wild bee diversity and/or dynamics (Hernandez et al. 2009; Fortel et al. 2014; Fischer et al. 2016; Leong et al. 2016; Baldock 2020), we expect that just a few might be proven as effective predictors of local differences in dynamic distribution patterns of *M. sculpturalis*. Probably the most relevant are features associated with gradients of urban temperature regimes – including heat island effects and associated shifts in local phenology of relevant plants. The bee phenology and the seasonal availability of food plants (either those foraged for pollen or as nectar sources) might be further modified by management regimes (watering, pruning etc.) of different urban settings. The main purpose of capturing such local differences – if shown significant – is to enable an accurate, while also feasible and rational framework for future monitoring schemes, i.e. for designing an appropriately stratified sampling (allowing for the minimal time investment etc.).

Noteworthy, even under dramatically reduced foraging opportunities on *S. japonicum* as the preferred food-plant, we could not detect the bee activity on alternative plants within the area. One such commonly available plant, *Lavandula*, is very frequently visited in the bee European range, second only to *S. japonicum* (cf. Ćetković et al. 2020: extracts from the ongoing study). In some country accounts, such as France (Le Féon et al. 2018) and Italy (Ruzzier et al. 2020), *Lavandula* was even ranked as first (based on all available records); however, more frequent casual encounters of *M. sculpturalis* in southern France and northern Italy became common only > 8 years upon respective first detections. Such a difference in visitation patterns between western Europe and Serbia was likely affected by a higher population abundance in areas where *M. sculpturalis* persisted for longer time periods. Its higher abundances could have promoted a spill-over effect of surplus bees, which were more easily attracted to other available plants, at least for nectar (*Lavandula* and *Buddleja* are probably not suitable as

pollen source – cf. Ćetković et al. 2020). Conversely, the lack of records on other plants in the Belgrade area may be indicative of the local bee population not yet reaching the level of abundance that could support spill-over effects.

Understanding of genuine plant usage patterns is important for improving *M. sculpturalis* early detectability, as well as for further monitoring of its population trends. The effect of concentration, herewith based specifically on a single key food plant, was crucial for this early mass recording. Without this effect, the initially slow population growth would translate into a prolonged accumulation of rare accidental records. For this reason, species detection in many areas commonly lags behind its actual establishment and expansion. Such detection patterns are documented elsewhere in Europe (cf. Le Féon et al. 2018; Lanner et al. 2020a; Ruzzier et al. 2020 etc.), but without any consideration of possible mechanisms behind these time lags (cf. Crooks 2005). In turn, our results further emphasise the relevance of *S. japonicum* as the single most important food plant for establishment and spreading of the bee, as well as for its efficient recording, at least when bee population levels are low. Despite quite numerous plant taxa listed in various treatises of bee-plant interactions, affiliation of *M. sculpturalis* with selected members of the Fabaceae plant family seems by far the most relevant for pollen provisioning (Ćetković at al. 2020; see also relevant references in Introduction). Furthermore, *S. japonicum* is the only widely available, mass-blooming and phenologically suitable representative of the large-flowered Fabaceae in the Belgrade area and a similar situation exists in many Serbian cities and towns. Thus, to enable the early detection and to improve the efficiency of surveillance efforts in areas of suspected bee presence (or expected arrival), attention should be focused on locations with easily accessible, but not excessively abundant and too widely dispersed, key plant resources. Most suitable test-locations might be small towns or villages with preferably just a few *S. japonicum* trees, surrounded by wider landscapes that are poor in any proven pollen-source plants. These situations might correspond with effects of concentration, documented herewith for Belgrade in 2019. However, a suitable approach is yet to be conceived for assessing the eventual spreading of *M. sculpturalis* through vast semi-natural or wilderness areas.

Several studies urged for the establishment of monitoring programmes to track the expansion and evaluate possible impacts of this rapidly spreading alien bee (Quaranta et al. 2014; Le Féon et al. 2018; IUCN 2020; Ruzzier et al. 2020; Ribas Marquès and Díaz Calafat 2021). So far, comprehensive studies in colonised regions of Europe were more extensively based on opportunistic recordings of nesting activity (within artificial or natural settings), often with a substantial involvement of citizen scientists or through casual/scattered public contributions to various internet-based data repositories (Le Féon et al. 2018; Lanner et al. 2020a, 2020b; Ruzzier et al. 2020; Westrich 2020). Nesting-based monitoring may be organised as spatially effective, providing that a sufficiently wide network of voluntary observers could be organised and motivated to install tailored nesting facilities around their homes/workplaces, to regularly observe various bee activities and to tediously document and report their recordings. However, this approach may not be uniformly feasible across Europe, due to

regionally variable citizen's attitudes or prior experiences (Pocock et al. 2018; Requier et al. 2020). Furthermore, it is possibly not best suited for the early phase of colonisation, due to the likely poor effectiveness in recording a too sparse bee activity density (i.e. poor effort-efficiency ratio). Therefore, it should be regarded as complementary to active and field-intensive surveying of focal plants and bee activities on flowers. Undoubtedly, the combination of both approaches will be needed for the evaluation of potential invasiveness of this first widespread alien bee in Europe.

Currently, we still lack an elaborate and comprehensive monitoring protocol – generally for any of the alien bee species worldwide. In this study, we propose a set of surveying routines and analytical approaches suitable for a structured assessment of plant resource availability, integrated with a standardised quantification of sculptured resin bee activity density. To build a functional monitoring approach, this working framework requires further testing and quantitative "calibration" of suggested procedures, under different environmental settings and varied modalities specific for each local or regional colonisation event. This should be based on extensive comparison of future assessment trials, taking into account the complicated interplay of resources: the co-occurrence of favourable plants (of different functional status: pollen or nectar-only sources), their varying phenologies and management regimes at different scales (from landscape through to regional), affected by varying environmental gradients (from urban to natural), while also considering particular establishment histories.

Regional context: introduction and expansion within SE Europe

The first three occurrences of *M. sculpturalis* east of the Alps, as documented during 2015–2017 (NE Hungary, N Serbia and NE Austria), were remarkably distant from the contemporary W European range and also widely mutually separated across the Pannonian Plain (Suppl. material 1). Accordingly, all were considered as likely cases of long-distance jump dispersal (Kovács 2015; Ćetković and Plećaš 2017; Lanner et al. 2020a), relative to a largely continuous range expansion within W Europe. Further to the east, the position of the sole record in Romania (from 2019) matches the relative distances of dispersal events of 2015–2017, while the dispersal jump to Crimea (in 2018) was outstandingly long-distant. Therefore, the overall pattern of this "SE European phase" of *M. sculpturalis* expansion appears as surprisingly different from the dispersal history in W Europe during 2008–2019 (cf. Ćetković et al. 2020; Suppl. material 1). Herewith, we consider the elements of alternative regional introduction and expansion scenarios.

From this wider perspective, a long-distance jump into Belgrade indeed seems as the most plausible scenario. The status of Belgrade (the capital city) and its position at important traffic junctions of several major routes from central and western Europe, makes it highly exposed to a large-scale transportation of diverse goods (Suppl. material 2: Fig. S2.1). The lack of records from most of Serbia and also from most of neighbouring countries, might further support the hypothesis that Belgrade was the genuine introduction point for Serbia (and for the Central Balkans). However, the initial dispersal

distances of elaborated SE European cases do not allow for more specific inferences regarding the origin. Generally, human-aided secondary introductions amongst the recently established, but widely isolated locations within SE Europe are not likely, since the initial low-abundances reduce the chances for inadvertent passive transportations (Bertelsmeier and Keller 2018). Therefore, the source(s) of these presumed long-distance jumps within SE Europe could have been any population from the earlier-established W European range; even the overseas origins cannot be excluded (Kovács 2015). The recent estimates of genetic relatedness suggest that the introduction into NE Austria represents an independent colonisation event in Europe, i.e. not originating from populations established in France and Switzerland (Lanner et al. 2021).

However, an in-depth consideration of two contrasting cases (Belgrade vs. E Pannonian) suggests that the alternative scenario of the colonisation of N Serbia is even more plausible; it is based primarily on a diffusive mode of spreading (Suarez et al. 2001). The vivid nesting activity of *M. sculpturalis* in the small Hungarian town of Gyöngyös (Kovács 2015) indicates that local establishment has happened in one or more seasons before the actual detection. Its likely longer and more extended presence in the NE Pannonian Region is further emphasised with predominance of nesting-based records over the plant-based ones in reports from 2018. The seemingly abrupt expansion of its apparent range across the NE Pannonian Plain in 2018, only three years after the first detection, cannot be based on further human-assisted jump dispersal events. More likely, a slow "sneaking" diffusive dispersal was taking place almost continuously for several years, probably for a much longer period than could be inferred from the available recordings. Accordingly, before more substantial abundances could become obvious (simultaneously throughout the region), the southward spreading across the Pannonian lowlands could have already reached the northern Balkans (i.e. Serbia in 2017), without being detected in the intermediary area before 2018. Therefore, the impression of a genuine, fairly distant jump into Belgrade, unrelated to the prior introduction in NE Hungary, is most probably an artifact, i.e. the "type III" lag phase (Hui and Richardson 2017, after Crooks 2005). Somewhat contrasting evidence of *M. sculpturalis* spreading patterns at two analysed spatio-temporal scales (local vs. regional) indicates that it lacks the true lag phase (i.e. the "type II" of Hui and Richardson 2017). The usually slow initial population build-up apparently does not hamper the active and successful spreading of this bee, but coupled with a relatively scattered faunistic research in the area, it resulted in a poor detection in the region during at least three years (since 2015). Noteworthy, the widespread presence (since 2018) was documented merely through accidental/casual activity of citizen scientists (Rovarok, pókok 2017–2019; Insekti Srbije 2018; izeltlabuak.hu 2018), i.e. without any focused research.

The recognition of one vs. another mode of dispersal, as well as the identification of a probable introduction and expansion pathway(s), may be severely difficult and often speculative, but nevertheless highly important for understanding the spatio-temporal patterns of each non-native colonisation (Suarez et al. 2001; Trakhtenbrot et al. 2005; Hui and Richardson 2017). Herewith, we contrasted the evidence from methodologically different approaches (focused/systematic surveillance, based on focal

plant resources and casual/opportunistic recording through unfocused citizen observations) at two similar temporal scales (3 vs. 5+ years), but over largely different spatial scales (< 20 km vs. > 300 km). The study revealed somewhat contrasting, but complementary expansion and detection patterns, as important aspects of usually hidden early colonisation dynamics, which are of great methodological relevance for future monitoring. We suggest that, in the case of the bee with relatively narrow and well-established trophic requirements, focusing on key floral resources and concentration-dilution effects is a highly profitable approach. Nevertheless, the evidence lacking this component may be highly useful in reconstruction of expansion modes and pathways, if interpreted within a suitable spatio-temporal framework and well-understood recording context. The source of *M. sculpturalis* SE European introduction(s) would be more conclusively identified with a molecular genetic approach (Bila Dubaić and Lanner 2021; Lanner et al. 2021), which will provide a better understanding of dispersal modes and general pathways. However, fine-scale exploratory studies focused on revealing the regional expansion dynamics and patterns of local interactions will remain a highly relevant approach for establishing efficient detection and surveillance.

Finally, we have shown that, contrary to common expectations (Quaranta et al. 2014; Lanner et al. 2020a), the striking appearance and easy to observe behaviour of *M. sculpturalis* is not sufficient to ensure the very early detection and real-time tracking, without a specifically tailored surveillance approach. However, this bee represents a highly suitable and prospective model organism for comprehensive studies of non-native bee colonisations.

Acknowledgements

Authors JBD, MP, JR and AĆ were partly supported through the long-term project funded by the Ministry of Education, Science and Technological Development of the Republic of Serbia (# III43001: 2011–2019; # 451-03-68/2020-14/200178: 2020); JL was partly supported by a DOC Fellowship of the Austrian Academy of Sciences at the Institute of Integrative Nature Conservation Research at the University of Natural Resources and Life Sciences. We would like to express our gratitude to the editor and two anonymous reviewers for their detailed feedback and highly constructive suggestions which significantly improved our manuscript. We are thankful to Dr. Jasmina Krpo-Ćetković who critically read our manuscript and helped us during the revision process.

References

Aguado O, Hernández-Castellano C, Bassols E, Miralles M, Navarro D, Stefanescu C, Vicens N (2018) *Megachile* (*Callomegachile*) *sculpturalis* Smith, 1853 (Apoidea: Megachilidae): a new exotic species in the Iberian Peninsula, and some notes about its biology. Butlletí de la Institució Catalana d'Història Natural 82: 157–162.

Aizen MA, Arbetman MP, Chacoff NP, Chalcoff VR, Feinsinger P, Garibaldi LA, Harder LD, Morales CL, Sáez A, Vanbergen AJ (2020) Invasive bees and their impact on agriculture. [Chapter 2] In: Bohan DA, Vanbergen AJ (Eds) The future of agricultural landscapes, Part I. Advances in Ecological Research 63: 49–92. https://doi.org/10.1016/bs.aecr.2020.08.001

Amiet F (2012) Kurzbeitrag Die Blattschneiderbiene *Megachile sculpturalis* Smith, 1853 (Hymenoptera, Apidae) nun auch in der Schweiz. Entomo Helvetica 5: 157–159.

Andrieu-Ponel V, Ponel P, Le Féon V, Geslin B, Duvallet G (2018) À propos du comportement de butinage de *Megachile sculpturalis* Smith, 1853, en France méditerranéenne (Nîmes et Montpellier) (Hymenoptera, Megachilidae). Bulletin de la Société Entomologique de France 123(1): 49–54. https://doi.org/10.32475/bsef_1984

Ascher JS, Pickering J (2020) Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species [Accessed: November, 2020]

Ascher JS, Pickering J (2021) *Megachile sculpturalis* Smith, 1853. In: Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). https://www.discoverlife.org/mp/20q?search=Megachile+sculpturalis#Hosts [Accessed: April, 2021]

Baldock KCR (2020) Opportunities and threats for pollinator conservation in global towns and cities. Current Opinion in Insect Science 38: 63–71. https://doi.org/10.1016/j.cois.2020.01.006

Barraclough RK (2000) Distance sampling: a discussion document produced for the Department of Conservation. Science & Research Internal Reports 175. Department of Conservation, Auckland, New Zealand.

Batra SWT (1998) Biology of the giant resin bee, *Megachile sculpturalis* Smith, a conspicuous new immigrant in Maryland. Maryland Naturalist 42: 1–3.

Bertelsmeier C, Keller L (2018) Bridgehead effects and role of adaptive evolution in invasive populations. Trends in Ecology & Evolution 33(7): 527–534. https://doi.org/10.1016/j.tree.2018.04.014

Bila Dubaić J, Lanner J (2021) *Megachile sculpturalis* (Hymenoptera: Megachilidae): a valuable study organism for invasive pollinators and the role of beekeepers in ongoing monitoring programs. Bee World 98(3): 78–82. https://doi.org/10.1080/0005772X.2021.1940580

Bila Dubaić J, Raičević J, Plećaš M, Lanner J, Nikolić P, Žikić V Stanisavljević Lj, Ćetković A (2021) Further range expansion of the sculptured resin bee (*Megachile sculpturalis*) in Serbia and Bosnia & Herzegovina. Acta entomologica serbica 26: 37–63. https://doi.org/10.5281/zenodo.5537059

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarosik V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends in Ecology & Evolution 26(7): 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Bortolotti L, Luthi F, Flaminio S, Bogo G, Sgolastra F (2018) First record of the Asiatic bee *Megachile disjunctiformis* in Europe. Bulletin of Insectology 71: 143–149.

Campbell JW, Campbell BE, Kimmel CB, Galvan P (2016) Observations of insect visitors to Price's Potato Bean (*Apios priceana*, Fabaceae) in North Alabama, USA. Plant Ecology and Evolution 149(3): 316–318. https://doi.org/10.5091/plecevo.2016.1232

Ćetković A, Plećaš M (2017) Dalje širenje alohtone azijske pčele u Evropi: prvi nalaz *Megachile sculpturalis* na Balkanu. In: XI Simpozijum entomologa Srbije 2017, Goč, Zbornik rezimea. Entomološko društvo Srbije, 82–83. http://www.eds.org.rs/SES/2017/SES_2017_Zbornik.pdf

Ćetković A, Stanisavljević L, Plećaš M, Raičević J, Žikić V, Glavendekić M, Bila Dubaić J (2020) Project: Monitoring the spread of sculptured resin bee (*Megachile sculpturalis*) in Serbia. Centar za biologiju pčela. Biološki fakultet Univerzitet u Beogradu. https://sites.google.com/bio.bg.ac.rs/srbee/english?authuser=0 [Accessed: March, 2021]

Cohen H, Philpott SM, Liere H, Lin BB, Jha S (2020) The relationship between pollinator community and pollination services is mediated by floral abundance in urban landscapes. Urban Ecosystems 24(2): 275–290. https://doi.org/10.1007/s11252-020-01024-z

Courchamp F, Fournier A, Bellard C, Bertelsmeier C, Bonnaud E, Jeschke JM, Russell JC (2017) Invasion biology: Specific problems and possible solutions. Trends in Ecology & Evolution 32(1): 13–22. https://doi.org/10.1016/j.tree.2016.11.001

Crone EE (2013) Responses of social and solitary bees to pulsed floral resources. American Naturalist 182(4): 465–473. https://doi.org/10.1086/671999

Crooks JA (2005) Lag times and exotic species: The ecology and management of biological invasions in slow-motion. Ecoscience 12(3): 316–329. https://doi.org/10.2980/i1195-6860-12-3-316.1

Dillier F-X (2016) Eingeschleppte Asiatische Mörtelbiene *Megachile sculpturalis* Smith, 1853 (Hymenoptera, Apidae) erstmals nördlich der Alpen gesichtet. Entomo Helvetica 9: 153–156.

Fischer LK, Eichfeld J, Kowarik I, Buchholz S (2016) Disentangling urban habitat and matrix effects on wild bee species. PeerJ 4: e2729. https://doi.org/10.7717/peerj.2729

Fitch G, Wilson CJ, Glaum P, Vaidya C, Simao M-C, Jamieson MA (2019) Does urbanization favour exotic bee species? Implications for the conservation of native bees in cities. Biology Letters 15(12): e20190574. https://doi.org/10.1098/rsbl.2019.0574

Fortel L, Henry M, Guilbaud L, Guirao AL, Kuhlmann M, Mouret H, Rollin O, Vaissière BE (2014) Decreasing abundance, increasing diversity and changing structure of the wild bee community (Hymenoptera: Anthophila) along an urbanization gradient. PLoS ONE 9(8): e104679. https://doi.org/10.1371/journal.pone.0104679

Gaston AJ, Collins BL, Diamond AW (1987) The "Snapshot" count for estimating densities of flying seabirds during boat transects: A cautionary comment. The Auk 104(2): 336–338. https://doi.org/10.1093/auk/104.2.336

Gathmann A, Tscharntke T (2002) Foraging ranges of solitary bees. Journal of Animal Ecology 71(5): 757–764. https://doi.org/10.1046/j.1365-2656.2002.00641.x

Geslin B, Gachet S, Deschamps-Cottin M, Flacher F, Ignace B, Knoploch C, Meineri É, Robles C, Ropars L, Schurr L, Le Féon V (2020) Bee hotels host a high abundance of exotic bees in an urban context. Acta Oecologica 105: e103556. https://doi.org/10.1016/j.actao.2020.103556

Gogala A, Zadravec B (2018) First record of *Megachile sculpturalis* Smith in Slovenia (Hymenoptera: Megachilidae). Acta Entomologica Slovenica (Ljubljana) 26: 79–81.

Google Inc. (2020) Google Earth Pro ver. 7.3.3.7786. https://www.google.com/earth/ [accessed March, 2021]

Goulson D (2003) Effects of introduced bees on native ecosystems. Annual Review of Ecology, Evolution, and Systematics 34(1): 1–26. https://doi.org/10.1146/annurev.ecolsys.34.011802.132355

Greene T, Efford M (2012) Birds: estimates of absolute density and abundance – distance sampling. Inventory and monitoring toolbox: birds, DOCDM-534993 (v.1.0). Department of Conservation, Auckland, New Zealand.

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153(3): 589–596. https://doi.org/10.1007/s00442-007-0752-9

Guariento E, Lanner J, Staggl MA, Kranebitter P (2019) *Megachile sculpturalis* (Smith, 1853) (Hymenoptera: Megachilidae), the giant resin bee new to South Tyrol with a newly described plant species interaction. Gredleriana 19: 209–215. https://doi.org/10.5281/zenodo.3565365

Hall HG, Avila L (2016) *Megachile sculpturalis*, the Giant Resin Bee, overcomes the blossom structure of Sunn Hemp (*Crotalaria juncea*) that impedes pollination. Journal of Melittology 65(65): 1–11. https://doi.org/10.17161/jom.v0i65.5887

Hernandez JL, Frankie GW, Thorp RW (2009) Ecology of urban bees: A review of current knowledge and directions for future study. Cities and the Environment 2(1): 3–3. https://doi.org/10.15365/cate.2132009

Hinojosa-Diaz IA, Yanez-Ordonez O, Chen G, Peterson AT, Engel MS (2005) The North American invasion of the giant resin bee (Hymenoptera: Megachilidae). Journal of Hymenoptera Research 14: 69–77.

Hoffmann BD, Courchamp F (2016) Biological invasions and natural colonisations: Are they that different? NeoBiota 29: 1–14. https://doi.org/10.3897/neobiota.29.6959

Hui C, Richardson MD (2017) Invasion dynamics. Oxford University Press, 322 pp. https://doi.org/10.1093/acprof:oso/9780198745334.001.0001

Hymenopterists Forum (2019) Stefan-Fotin, Alexandru: Romania, Bucharest, 16.07.2019, *Megachile sculpturalis* [det. by Vereecken N. 2019]. Hymenopterists Forum – private Facebook group. https://www.facebook.com/photo/?fbid=2295375623879014&set=pcb.1627477290719458 [Accessed: December, 2021]

Insekti Srbije (2018) Cvjetićanin Miloš: Da li je ovo mamutska osa? Park prirode "Palić", 28. jul 2018, https://www.facebook.com/groups/insectserbia/permalink/1052703608266051/; https://youtu.be/Qi_ikI9RjLw, Insects of Serbia – public Facebook group. [Accessed: September, 2020]

IUCN (2020) Managing invasive alien species to protect wild pollinators. Technical guidance prepared for the European Commission under contract No +07.0202/2018/795538/SER/ENV.D.2 "Technical support related to the implementation of the EU Pollinators Initiative". European Commission, 43 pp.

Ivanov SP, Fateryga AV (2019) First record of the invasive giant resin bee *Megachile* (*Callomegachile*) *sculpturalis* Smith, 1853 (Hymenoptera: Megachilidae) in the Crimea. Far Eastern Entomologist = Dal'nevostochnyi Entomolog 395: 7–13. https://doi.org/10.25221/fee.395.2

izeltlabuak.hu (2018) Forum "Izeltlabuak.hu, segítünk egymásnak megismerni Magyarország ízeltlábú élővilágát" [Izeltlabuak.hu: we help each other get to know the arthropods of Hungary] https://www.izeltlabuak.hu, https://www.izeltlabuak.hu/talalat/33684, https://www.izeltlabuak.hu/talalat/33628, https://www.izeltlabuak.hu/talalat/33775, https://www.izeltlabuak.hu/talalat/33516. [Accessed: June, 2020]

Kovács T (2015) *Megachile sculpturalis* Smith, 1853 in Hungary (Hymenoptera, Megachilidae). Folia Historico-Naturalia Musei Matraensis 39: 73–76.

Lanner J, Huchler K, Pachinger B, Sedivy C, Meimberg H (2020a) Dispersal patterns of an introduced wild bee, *Megachile sculpturalis* Smith, 1853 (Hymenoptera: Megachilidae) in European alpine countries. PLoS ONE 15(7): e0236042. https://doi.org/10.1371/journal.pone.0236042

Lanner J, Meyer P, Harmetzky F, Meimberg H, Pachinger B (2020b) Die Asiatische Mörtelbiene (Hymenoptera: *Megachile sculpturalis* Smith, 1853) – eine neue Bienenart für Österreich. Beiträge zur Entomofaunistik 21: 87–95.

Lanner J, Gstöttenmayer F, Curto M, Geslin B, Huchler K, Orr MC, Pachinger B, Sedivy C, Meimberg H (2021) Evidence for multiple introductions of an invasive wild bee species currently under rapid range expansion in Europe. BMC Ecology and Evolution 21(1): e17. https://doi.org/10.1186/s12862-020-01729-x

Le Féon V, Geslin B (2018) Écologie et distribution de l'abeille originaire d'Asie *Megachile sculpturalis* Smith 1853 (Apoidea – Megachilidae – Megachilini): Un état des connaissances dix ans après sa première observation en Europe. Osmia 7: 31–39. https://doi.org/10.47446/OSMIA7.6

Le Féon V, Aubert M, Genoud D, Andrieu-Ponel V, Westrich P, Geslin B (2018) Range expansion of the Asian native giant resin bee *Megachile sculpturalis* (Hymenoptera, Apoidea, Megachilidae) in France. Ecology and Evolution 8(3): 1534–1542. https://doi.org/10.1002/ece3.3758

LeCroy KA, Savoy-Burke G, Carr DE, Delaney DA, Roulston TH (2020) Decline of six native mason bee species following the arrival of an exotic congener. Scientific Reports 10(1): e18745. https://doi.org/10.1038/s41598-020-75566-9

Leong M, Ponisio LC, Kremen C, Thorp RW, Roderick GK (2016) Temporal dynamics influenced by global change: Bee community phenology in urban, agricultural, and natural landscapes. Global Change Biology 22(3): 1046–1053. https://doi.org/10.1111/gcb.13141

MacIvor JS, Packer L (2015) 'Bee hotels' as tools for native pollinator conservation: A premature verdict? PLoS ONE 10(3): e0122126. https://doi.org/10.1371/journal.pone.0122126

Maeta Y, Kitamura K, Kagino Y, Ikegami N (2008) In-nest behaviors and labor economy of *Megachile* (*Callomegachile*) *sculpturalis* Smith (Hymenoptera, Megachilidae). Chugoku Kontyu 22: 1–22.

Mangum WA, Brooks RW (1997) First records of *Megachile* (*Callomegachile*) *sculpturalis* Smith (Hymenoptera: Megachilidae) in the continental United States. Journal of the Kansas Entomological Society 70: 140–142.

Mangum WA, Sumner S (2003) A survey of the North American range of *Megachile* (*Callomegachile*) *sculpturalis*, an adventive species in North America. Journal of the Kansas Entomological Society 76: 658–662.

Michener CD (2007) The bees of the world. [2nd edn.]. The Johns Hopkins University Press, Baltimore, 953 [+ xviii] pp.

Monselise SP, Goldschmidt EE (1982) Alternate bearing in fruit trees. Horticultural Reviews 4: 128–173. https://doi.org/10.1002/9781118060773.ch5 [Chapter 5]

Morales CL, Sáez A, Garibaldi LA, Aizen MA (2017) Disruption of pollination services by invasive pollinator species. [Chapter 13]. In: Vilà M, Hulme PE (Eds) Impact of biological invasions on ecosystem services. Springer International Publishing, Switzerland, 203–220. https://doi.org/10.1007/978-3-319-45121-3_13

Nikolić P (2020) Sculptured Resin Bee (*Megachile sculpturalis*). Observed on: August 3, 2020: Banja Luka 78000, Bosnia and Herzegovina. https://www.inaturalist.org/observations/55266322 [Accessed: August, 2020]

Ortiz-Sánchez FJ, Navarro JF, Taeger U (2018) *Megachile* (*Callomegachile*) *sculpturalis* Smith, 1853, nueva especie para la fauna Ibérica (Hymenoptera, Megachilidae). Boletin de la SEA 63: 259–261.

Parys K, Tripodi AD, Sampson BJ (2015) The giant resin bee, *Megachile sculpturalis* Smith: New distributional records for the mid- and gulf-south USA. Biodiversity Data Journal 3: e6733. https://doi.org/10.3897/BDJ.3.e6733

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2020) Pinhnlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-144. https://CRAN.R-project.org/package=nlme

"pitrusque" (2019) Sculptured Resin Bee (*Megachile sculpturalis*). Observed on August 5, 2019: 21000, Split, Croatie. https://www.inaturalist.org/observations/37059640 [Accessed: February 2020]

Pocock MJO, Chandler M, Bonney R, Thornhill I, Albin A, August T, Bachman S, Brown PMJ, Cunha DGF, Grez A, Jackson C, Peters M, Rabarijaon NR, Roy HE, Zaviezo T, Danielsen F (2018) A vision for global biodiversity monitoring with citizen science. Advances in Ecological Research 59: 169–223. https://doi.org/10.1016/bs.aecr.2018.06.003 [Chapter 6 in: Next generation biomonitoring: part 2. Bohan DA, Dumbrell AJ, Woodward G, Jackson M (Eds)]

Poggi R, Tavano ML, Bonifacino M (2020) Reperti liguri di *Megachile* (*Callomegachile*) *sculpturalis* Smith, 1853 (Hymenoptera, Megachilidae). Doriana (Genova) 9: 1–6.

Poulsen NR, Rasmussen C (2020) Island bees: Do wood nesting bees have better island dispersal abilities? Apidologie 51(6): 1006–1017. https://doi.org/10.1007/s13592-020-00778-x

Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, van Kleunen M, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. Biological Reviews of the Cambridge Philosophical Society 95(6): 1511–1534. https://doi.org/10.1111/brv.12627

QGIS Development Team (2018) QGIS Geographic Information System. Open Source Geospatial Foundation. http://qgis.org

Quaranta M, Sommaruga A, Balzarini P, Felicioli A (2014) A new species for the bee fauna of Italy: *Megachile sculpturalis* continues its colonization of Europe. Bulletin of Insectology 67: 287–293.

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rasmont P, Devalez J, Pauly A, Michez D, Radchenko VG (2017) Addition to the checklist of IUCN European wild bees (Hymenoptera: Apoidea). Annales de la Société entomologique de France (NS) 53: 17–32. https://doi.org/10.1080/00379271.2017.1307696

Requier F, Andersson GKS, Oddi FJ, Garibaldi LA (2020) Citizen science in developing countries: How to improve volunteer participation. Frontiers in Ecology and the Environment 18(2): 101–108. https://doi.org/10.1002/fee.2150

Resl J (2018) *Megachile* (*Callomegachile*) *sculpturalis* Smith, 1853. In: Scarabaeidae; Aktivity; Zajímavé objevy. https://www.scarabaeidae.cz/products/megachile-callomegachile-sculp-

turalis-smith-1853/, http://files.listorozi.webnode.cz/200000105-50fb451f64/Megachilidae%20moje.pdf. [Accessed: January, 2021]

Ribas Marquès E, Díaz Calafat J (2021) The Asian giant resin bee *Megachile sculpturalis* Smith 1853 (Hymenoptera: Apoidea: Megachilidae), a new exotic species for the bee fauna of Mallorca (Balearic Islands, Spain). Journal of Apicultural Research 60(3): 506–511. https://doi.org/10.1080/00218839.2021.1874177

Rovarok, pókok (2017–2019) Facebook group "Rovarok, pókok" [Insects, spiders]. https://www.facebook.com/groups/rovarokpokok/ [Accessed: January 2021]

Russo L (2016) Positive and negative impacts of non-native bee species around the world. Insects 7(4): e69. https://doi.org/10.3390/insects7040069

Ruzzier E, Menchetti M, Bortolotti L, Selis M, Monterastelli E, Forbicioni L (2020) Updated distribution of the invasive *Megachile sculpturalis* (Hymenoptera: Megachilidae) in Italy and its first record on a Mediterranean island. Biodiversity Data Journal 8: e57783. https://doi.org/10.3897/BDJ.8.e57783

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pysek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jager H, Kartesz J, Kenis M, Kreft H, Kuhn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Stajerova K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. Nature Communications 8(1): e14435. https://doi.org/10.1038/ncomms14435

Sheffield CS, Ratti C, Packer L, Griswold TL (2011) Leafcutter and mason bees of the genus *Megachile* Latreille (Hymenoptera: Megachilidae) in Canada and Alaska. Canadian Journal of Arthropod Identification 18: 1–107. https://doi.org/10.3752/cjai.2011.18

Steckel J, Westphal C, Peters MK, Bellach M, Rothenwoehrer C, Erasmi S, Scherber C, Tscharntke T, Steffan-Dewenter I (2014) Landscape composition and configuration differently affect trap-nesting bees, wasps and their antagonists. Biological Conservation 172: 56–64. https://doi.org/10.1016/j.biocon.2014.02.015

Steffan-Dewenter I, Münzenberg U, Bürger C, Thies C, Tscharntke T (2002) Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83(5): 1421–1432. https://doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2

Stout JC, Morales CL (2009) Ecological impacts of invasive alien species on bees. Apidologie 40(3): 388–409. https://doi.org/10.1051/apido/2009023

Straffon-Díaz S, Carisio L, Manino A, Biella P, Porporato M (2021) Nesting, sex ratio and natural enemies of the giant resin bee in relation to native species in Europe. Insects 12(6): e545. https://doi.org/10.3390/insects12060545

Suarez AV, Holway DA, Case TJ (2001) Patterns of spread in biological invasions dominated by long-distance jump dispersal: Insights from Argentine ants. Proceedings of the National Academy of Sciences of the United States of America 98(3): 1095–1100. https://doi.org/10.1073/pnas.98.3.1095

Tepedino VJ, Stanton NL (1981) Diversity and competition in bee–plant communities on short-grass prairie. Oikos 36(1): 35–44. https://doi.org/10.2307/3544376

Trakhtenbrot A, Nathan R, Perry G, Richardson DM (2005) The importance of long-distance dispersal in biodiversity conservation. Diversity & Distributions 11(2): 173–181. https://doi.org/10.1111/j.1366-9516.2005.00156.x

Vanbergen AJ, Espindola A, Aizen MA (2018) Risks to pollinators and pollination from invasive alien species. Nature Ecology & Evolution 2(1): 16–25. https://doi.org/10.1038/s41559-017-0412-3

Vereecken NJ, Barbier E (2009) Premières données sur la présence de l'abeille asiatique *Megachile* (*Callomegachile*) *sculpturalis* Smith (Hymenoptera, Megachilidae) en Europe. Osmia 3: 4–6. https://doi.org/10.47446/OSMIA3.3

Westrich P (2017) Erstnachweis der Asiatischen Mörtelbiene (*Megachile sculpturalis*) in Österreich! [Projekte *Megachile sculpturalis* 7]. https://www.wildbienen.info/forschung/projekte_17.php [Accessed: August, 2019]

Westrich P (2020) Neues zur Ausbreitung der Mörtelbiene *Megachile sculpturalis* Smith 1853 (Hymenoptera: Anthophila) in Deutschland – Stand Oktober 2019. Eucera 14: 12–15.

Westrich P, Knapp A, Berney I (2015) *Megachile sculpturalis* Smith 1853 (Hymenoptera, Apidae), a new species for the bee fauna of Germany, now north of the Alps. Eucera 9: 3–10.

Wu Y-R (2006) Hymenoptera, Megachilidae. Fauna Sinica, Insecta. Vol. 44. [In Chinese, English summary]. Science Press, Beijing, 474 pp.

Supplementary material 1

Megachile sculpturalis distribution through Europe for the period 2011–2019

Authors: Jovana Bila Dubaić, Milan Plećaš, Jovana Raičević, Julia Lanner, Aleksandar Ćetković

Data type: map (.pdf file)

Explanation note: Summary visualisation of the *Megachile sculpturalis* distribution and spreading through Europe for the period 2011–2019, shown as series of tentative expansion phases.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.73.80343.suppl1

Supplementary material 2

Study area – Belgrade (Serbia): basic topography, biogeography, ecological patterns and urbanistic zonation

Authors: Jovana Bila Dubaić, Milan Plećaš, Jovana Raičević, Julia Lanner, Aleksandar Ćetković

Data type: maps (.pdf file)

Explanation note: Study area – Belgrade (Serbia): basic topography, biogeography, ecological patterns (habitats, land-use, landscapes) and urbanistic zonation: (i) City of Belgrade: general features (Fig. S2.1); (ii) Zonation of Belgrade (version_01: survey in 2019; Fig. S2.2); (iii) Survey design and processing of geospatial framework (Fig. S2.3) (This is the PDF version of selected pages from the thematic project website (Ćetković et al. 2020), by: Centre for Bee Research of the Faculty of Biology, University of Belgrade (available also at: https://srbee.bio.bg.ac.rs/english/belgrade-general-features; https://srbee.bio.bg.ac.rs/english/m-sculpturalis-2019-survey; with occasional updates).

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.73.80343.suppl2

Supplementary material 3

Quantitative survey of distribution and abundance parameters of *M. sculpturalis* and *S. japonicum* in the Belgrade area in August 2019

Authors: Jovana Bila Dubaić, Milan Plećaš, Jovana Raičević, Julia Lanner, Aleksandar Ćetković

Data type: spreadsheet database (excel file)

Explanation note: Quantitative survey of distribution and abundance parameters of *M. sculpturalis* (BpM) and *S. japonicum* (NoT, NoT_iB, TFR, CFR) in the Belgrade area in August 2019: Tables S3.1–S3.4.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.73.80343.suppl3

Supplementary material 4

Records of *M. sculpturalis* from the broader SE European region (compiled for: 2015–2019)

Authors: Jovana Bila Dubaić, Milan Plećaš, Jovana Raičević, Julia Lanner, Aleksandar Ćetković

Data type: database (excel file)

Explanation note: Table S4.1. Records of *M. sculpturalis* from the broader SE European region and the adjacent areas (compiled for: 2015–2019). Table S4.2. Published data sources used.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.73.80343.suppl4

Supplementary material 5

Results of statistical testing and distribution maps of estimated metrics

Authors: Jovana Bila Dubaić, Milan Plećaš, Jovana Raičević, Julia Lanner, Aleksandar Ćetković

Data type: maps (.pdf file)

Explanation note: Belgrade area: results of statistical testing (Tables S5.1–S5.3) and distribution maps of estimated metrics (Figs S5.1–S5.2).

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.73.80343.suppl5